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Mesozoic Velocipedinae (Nabidae s.l.) and Ceresopseidae (Reduvioidea), with notes on the phylogeny of Cimicomorpha (Heteroptera)

Мезозойские Velocipedinae (Nabidae s.l.) и Ceresopseidae (Reduvioidea), с замечаниями о филогении Cimicomorpha (Heteroptera)

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KEY WORDS: Heteroptera, Cimicomorpha, Nabidae, Velocipedinae, Reduvioidea, Ceresopseidae, Leptopodomorpha, fossil, phylogeny, venation, Mesozoic, Jurassic, Cretaceous.

КЛЮЧЕВЫЕ СЛОВА: Heteroptera, Cimicomorpha, Nabidae, Velocipedinae, Reduvioidea, Ceresopseidae, Leptopodomorpha, ископаемые, филогения, жилкование, мезозой, юра, мел.

ABSTRACT. New Mesozoic true bugs assigned to paraphyletic Velocipedinae s.l. of paraphyletic Nabidae s.l. are described in Darniopseini **stat.n.** (Jurassic: *Juracipeda popovi* **gen.** et **sp.n.** from Yakutia and *Saldonabis proteus* **gen.** et **sp.n.** from Kyrgyzstan) and Vetanthocorini (Early Cretaceous of Mongolia: *Izinabis kerzhneri* **gen.** et **sp.n.**). Vetanthocorini (originally described in Vetanthocoridae within Anthocoridae s.l.) are transferred into Velocipedinae and partly bridge the gap between Darniopseini plus modern Velocipedini on the one hand, and (1) remaining Nabidae and (2 — via *Curvicaudus* Yao, Cai et Ren, 2006) Anthocoridae s.l. on the other hand (second tribe assigned to Vetanthocoridae, Crassicerini, does not belong in Cimicoidea s.l.). The Early Jurassic genus *Darniopsis* Becker-Migdisova, 1958 and the family Ceresopseidae (assigned to Reduvioidea) are redescribed. The fossils indicate that two lineages of Cimicomorpha, Nabidae s.l. and Reduvioidea are traceable back to leptopodoid ancestors, making the Cobben's [1968] opinion on polyphyly of the infraorder more probable. Jurassic Pterocimicidae are transferred to Nepomorpha. Hemelytral venation of Heteroptera is discussed. Mesozoic finds confirm the Kerzhner's [1981] concept on transformation of the membrane venation in Cimicomorpha ('live' cells at the base of membrane being ousted by more distal 'dead' cells and veins), except for Reduvioidea (having 'live' cells expanded and possibly turning 'dead').

РЕЗЮМЕ. Новые мезозойские клопы, отнесённые к парафилетическому подсемейству Velocipedinae s.l. парафилетического семейства Nabidae s.l., описаны в составе Darniopseini **stat.n.** (юрские *Juracipeda popovi* **gen.** et **sp.n.** из Якутии и *Saldonabis proteus* **gen.** et **sp.n.** из Киргизии) и Vetanthocorini (раннемеловой *Izinabis kerzhneri* **gen.** et **sp.n.** из Монголии). Vetanthocorini (исходно описанные в составе Vetanthocoridae в пределах Anthocoridae s.l.) перенесены в Velocipedinae и отчасти заполняют промежуток между Darniopseini и современными Velocipedini с одной стороны и (1) остальными Nabidae и (2 — через *Curvicaudus* Yao, Cai et Ren, 2006) Anthocoridae s.l. с другой (вторая триба, описанная в Vetanthocoridae, Crassicerini, не относится к Cimicoidea s.l.). Переописаны раннеюрские род *Darniopsis* Becker-Migdisova, 1958 и семейство Ceresopseidae, отнесённое к Reduvioidea. Эти ископаемые позволяют считать, что две эволюционные линии Cimicomorpha, Nabidae s.l. и Reduvioidea, прослеживаются вглубь до лептоподоидных предков, что говорит в пользу мнения о полифилии этого инфраотряда [Cobben, 1968]. Юрские Pterocimicidae перенесены в Nepomorpha. Обсуждается жилкование переднего крыла Heteroptera. Мезозойские находки подтверждают предложенную И.М. Кержнером [1981] концепцию преобразования жилкования перепоночки у цимикоморф ("живые" ячейки в основании перепоночки вытесняются "мёртвыми" ячейками и жилками), за исключением Reduvioidea (у которых "живые" ячейки увеличились и возможно "омертвели").

Introduction

Velocipedinae Bergroth, 1891 (currently treated as a full family) is a small group in the modern fauna, comprising 30 species assigned to three genera, with Oriental distribution (from Nepal to the Solomon Isles) and little-known biology (collected on or under the bark, or under pieces of wood lying on the forest floor, sometimes from vegetation on river banks), good runners and fliers, predaceous, presumably using their exceptionally long rostrum to feed on some concealed food or prey (in soil, dead wood, etc.), and often bearing phoretic mites, apparently playing a role in their biology [Doesburg, 2004].

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The first representative of this group, *Scotomedes ater* Stål, 1873, was placed in Nabinae and overlooked by subsequent authors until Blöte [1945]. Bergroth [1891] described the next species as *Velocipeda prisca* Bergroth, 1891 in Saldidae, and created for it a subfamily Velocipedinae (treated as a family or tribe by subsequent authors few years later). Yet another species was published as *Godefridus alienus* Distant, 1904 in Reduviidae Apiomerinae (all three species now placed in the genus *Scotomedes* Stål, 1873). Kirkaldy [1908] noted that Velocipedinae are similar to Nabidae in the female genitalia and hemelytral venation, but retained the subfamily in Saldidae. Blöte [1945] transferred this subfamily (as Scotomedinae) to Nabidae, the view followed by Leston et al. [1954], Carayon [1970], and Kerzhner [1981].

Handlirsch [1906–1908: 1248] in his phylogeny of Hemipteroidea (based also on fossil evidence) placed Velocipedidae as the only direct survivors from the stock ancestral to most Gymnocerata (except for groups now united in Pentatomomorpha). Leston et al. [1954] divided Geocorisae (not mentioning Thaumastocoridae) into two infraorders, Pentotomomorpha and Cimicomorpha (assigning Nabidae Scotomedinae to the latter, and provisionally including Saldoidea into the former). Cobben [1968] regarded Pentotomomorpha as a natural group, and Cimicomorpha as polyphyletic, comprising at least three lineages descending separately from extinct Amphibicorisae: Reduvioidea, Thaumastocoroidea and Cimicoidea in the broadest sense (all remaining families; position of Pachynomidae intermediate between Reduvioidea and Cimicoidea; Joppeicidae left unplaced). Carayon [1977] divided Cimicomorpha (Thaumastocoridae not considered) into Reduvioidea (including Pachynomidae) and Cimicoidea in the broadest sense, and the latter into Miriformes and Cimiciformes (=Cimicoidea s.l. below).

Carayon [1977] recognized two basic types of the membrane veins, 'live' (bearing tracheae, nerves and sensillae) and 'dead' (fold-like). Following him, Kerzhner [1981] proposed a transformation sequence for the membrane venation in Cimicomorpha (cells formed by live veins being replaced by dead venation, sometimes also in cells) and considered Nabidae Velocipedinae to be the most primitive of living Cimicomorpha in the structure of rostrum and venation of membrane, and ancestral to remaining Cimicoidea s.l. and Reduvioidea.

Schuh and Štys [1991] rejected Kerzhner's theory of evolution of membrane veins, performed cladistic analysis of cimicomorphan families, treated Reduvioidea as the most basal lineage in Cimicomorpha, and divided Cimicoidea s.l. into Velocipedoidea (Velocipedidae, constituting the second basal lineage after reduvioids), Naboidea (Medocostidae and Nabidae), and Cimicoidea s.str. (six remaining cimicoid families).

Becker-Migdisova [1958] described several forewings from the Early Jurassic (about 195 Ma = million years ago; formerly considered latest Triassic) of Sogyuty at Issyk-Kul Lake, Kyrgyzstan (the site yielded more than 3600 insect fossils) as belonging to Membracidae, including *Darniopsis tragopea* Becker-Migdisova, 1958 and *Ceresopsis costalis* Becker-Migdisova, 1958 singled out into the subfamilies Darniopseinae and Ceresopseinae, respectively, and *Sphongophoriella reticulata* Becker-Migdisova, 1958 assigned to the extant tribe Hypsoprorini. Two more *Ceresopsis* species from the same site were added later [Becker-Migdisova, 1962].

Shcherbakov & Popov [2002: 148, 151] transferred Darniopseinae to Velocipedidae, raised Ceresopseinae to a full family (Heteroptera incertae infraordinis, possibly ancestral to Gerromorpha), and placed *Sphongophoriella* in Mesovelioidea (Mesoveliidae?); they also hypothesized that the first heteropterans (belonging to paraphyletic Nepomorpha) used their long probing rostrum to feed on soil invertebrates in the littoral zone (like Ochteridae, Saldidae and probably Velocipedidae) or inhabited floating plant carpets (like primitive Gerromorpha).

One more hemelytron from the same Early Jurassic site, and another from Kempendyai, Yakutia, dated presumably to latest Jurassic (about 150 Ma; the site yielded some 1200 fossil insects indicating Late Jurassic rather than Early Cretaceous age [Sinitshenkova, 1992]), represent two new genera similar to *Darniopsis* Becker-Migdisova, 1958 and described below. The new Early Jurassic genus is assigned to Nabidae s.l. with some reservations.

Numerous whole-bodied specimens of primitive Cimicomorpha from the Early Cretaceous Yixian Formation, Liaoning, China classified into 8 new genera and two tribes were assigned to a new family Vetanthocoridae in Anthocoridae s.l. by Yao et al. [2006] (the Jehol Group containing Yixian Formation is radiometrically dated 131–120 Ma, i.e. Late Hauterivian–Aptian [He et al., 2006], though many authors, including Yao et al. [2006], consider it Jurassic). Two specimens of Vetanthocorini from Hutel-Hara, Mongolia, dated presumably to earliest Cretaceous (this site yielded more than 3000 fossil insects that reveal Cretaceous rather than Jurassic affinities, and is considered the earliest Cretaceous in age [Ponomarenko, 1990, Rasnitsyn et al., 1998]), show much better preserved membrane venation with rudimentary live cells, long dead cells, and numerous dead veins. Based on this and other characters of hemelytra, antennae and male genitalia (see taxonomic part), this tribe (excluding *Liaoxia* Hong, 1987 and *Curvicaudus* Yao, Cai et Ren, 2006) is herein transferred to Velocipedinae s.l. Vetanthocorini partly bridge the gap between Darniopseinae and modern Velocipedinae, on the one hand, and remaining Nabidae s.l., on the other hand, confirming Kerzhner's [1981] views that these groups are closely related, enough to be united as a lineage traceable back to near the origins of Cimicomorpha, and that the membrane cells formed by live veins were ousted by dead venation in many cimicomorphan families. Therefore the classification of Nabidae s.l. (belonging to Cimicoidea s.l.) proposed by Kerzhner [1981] is followed herein, with subfamilies Nabinae, Prostemmatinae, Medocostinae, and Velocipedinae, and

the latter subfamily is extended to embrace, besides the extant tribe Velocipedini, two Mesozoic tribes, Darniopseini **stat.n.** and Vetanthocorini s.str.

The genus *Curvicaudus* similar to typical Vetanthocorini but showing several anthocorid traits presumably marks the origin of Anthocoridae s.l. from Velocipedinae s.l. Another tribe originally described in Vetanthocoridae, Crassicerini with three monobasic genera is dissimilar to the nominate tribe and poor in distinctive characters. Some of the genera assigned to it may even belong in Pentatomomorpha.

Monobasic Ceresopseidae from the same Early Jurassic site Sogyuty are similar to Darniopseini in the basic pattern of hemelytral venation, but share several traits with Reduviidae rather than with Nabidae s.l. and are therefore assigned to Reduvioidea.

Significance of these fossils for understanding the origins and phylogeny of Cimicomorpha is further discussed below.

All type specimens are kept in the Paleontological Institute, Russian Academy of Sciences, Moscow (PIN).

On hemelytral venation of Heteroptera

The forewing venation in true bugs is modified relative to their ancestors, hoppers of the extinct superfamily Scytinopteroidea (Homoptera: Auchenorrhyncha: Cicadomorpha s.l.), nevertheless, the comparison of primitive (especially Mesozoic) Leptopodoidea and some other bugs with their scytinopteroid precursors allows to elucidate some important points [Shcherbakov, 1996; Shcherbakov & Popov, 2002]. Only Scytinopteroidea share with Heteroptera possession of the costal (=cuneal=embolar) fracture, in addition to the medial (=corial) fracture developed in most Neoptera. The costal fracture is found in nearly all heteropteran infraorders, even in Pentatomomorpha (Mesozoic families: coreoid s.l. Pachymeridiidae and pentatomoid Mesopentacoridae [Shcherbakov & Popov, 2002: fig. 188]), but not known in Gerromorpha. With enlargement of the basal cell in true bugs, the costal fracture shifted distad, the medial one elongated, and both radial area (=discal cell 1) and medial area (=discal cell 2) shortened.

Contrary to the universally accepted homology, starting from Handlirsch [1906–1908], Tanaka [1926] and others [see China & Myers, 1929, and Schuh & Slater, 1995], in Heteroptera like in all other extant hemipteran groups the subcosta (except for its apex and sometimes base) is fused to (R+M)–R [Shcherbakov, 1996], not to the costal margin, and the subcostal trachea is reduced. We should follow Comstock & Needham [1898] and Reuter [1910] in taking the first hemelytral vein as costa. In Hemelytrata (=Auchenorrhyncha + Heteroptera) the costal vein usually bears two carinae (or laminae), precostal and hypocostal, sometimes one of them being reduced. The term 'embolium' is applied to this complex costal vein as seen in dorsal aspect [Schuh & Slater, 1995: fig. 10.1]. In Scytinopteroidea and Heteroptera the hypocostal lamina is provided with a subbasal hypocostal pit, to fix on the mesepimeral knob in repose (Druckknopfsystem [Cobben, 1957] = knob and socket [Gorb & Perez Goodwyn, 2003]). In some primitive true bugs and most scytinopteroids, arched lines run from the pit across the embolium which appears subdivided near its base. The free apex of Sc (separating from RA, the R stem, or even from R+M and running to C) looks like a third principal R branch, in addition to RA (=R1) and RP (=RS), and was usually designated as such; in true bugs it is the basalmost, often weakest anterior branch of R (termed R_a by Kerzhner [1981: figs 24, 26]). The term 'cuneus' is used for the anterodistal corner of corium cut off by the costal fracture, and 'exocorium' for the costal area (between C and Sc+R; sometimes erroneously termed 'embolium').

The live cells of the membrane, in Cimicomorpha maximum four in number, are fused or diminished in all groups of the infraorder, except for Reduviidae; membrane cells of Reduvioidea were coded as dead by Kerzhner [1981], but the veins delimiting them in Reduviidae are tracheated, similar to those bordering two live membrane cells in Miridae (see Leston [1962]). A deep similarity of the membrane venation in Reduviidae and Jurassic Cimicomorpha (Ceresopseidae and Velocipedinae Darniopseini, see below) further strengthens the opinion that the membrane cells in Reduviidae are homologous to the live membrane cells in Velocipedini and Miridae, not to the dead cells of Nabidae s.str. If even in mature adults of Reduviidae the veins delimiting membrane cells are not so well supplied by tracheae, nerves and sensillae as those in Miridae, it does not mean they are non-homologous, but just indicate their tracheae etc. are either underdeveloped or degrade soon after moulting to adult.

The anterior of the four membrane cells (cell 1) is closed by a thick (probably live) vein in *Darniopsis*, like in Leptopodoidea. In Velocipedini the cell 1 anterodistally is either closed by a dead vein continuing the live base (species of *Costomedes* Doesburg, 2004 [Doesburg, 2004: figs 26, 28]) or open (in the case the live 'stub vein' is retained). Such a sensillae-bearing stub (processus corial) is present in several cimicomorphan families, often persisting after reduction of live membrane cells. This stub was formed after the cell 1 had been opened distally; so far as in Reduvioidea this cell was obliterated without such opening (as evidenced by Ceresopseidae, see below), presumably no processus corial was ever present in this superfamily. In Tingoidea the vein closing the cell 1 ('stub vein') is fully developed and live, and all membrane cells are incorporated into the corium [Zhang et al., 2005]. Position of the corium/membrane boundary is not constant across Heteroptera (see below).

The anteriormost anal vein that became individualized in Neoptera is termed 'postcubitus' [Snodgrass, 1935]. In this nomenclature two claval veins in Hemiptera are Pcu and A1 (otherwise they are designated as A1 and A2).

Taxonomy

Cimicoidea Latreille, 1802, s.l.

Nabidae A.Costa, 1853, s.l.

Velocipedinae Bergroth, 1891

DIAGNOSIS. Hemelytra with costal area (=exocorium) wide, more than 1/3 width of hemelytron, concealing sides of abdomen in repose; costal margin usually convex. Embolium wide near base, edge of hypocostal lamina traversing R+M (running into basal cell in impression fossils). Costal (=cuneal) fracture long, straight, weakly inclined, directed toward near claval apex, ending not close to apex of basal cell and apex of medial (=corial) fracture. R with weak anterior branch (dSc) basal to costal fracture and often 1–2 in cuneus. Corium with broad basal cell and two discal cells. Four rather narrow cells in basal part of membrane (formed by live veins), anterior (cell 1) usually open or closed with dead vein apically. Clavus with commissural margin shorther than scutellar one; scutellar angle distinct. Hind tibia bearing stiff setae.

COMPOSITION. One extant and two Mesozoic tribes.

COMPARISON. Distinct from Medocostinae, Prostemmatinae, and Nabinae in the wide costal area, long costal fracture, and four live cells on membrane. More similar to primitive Leptopodoidea in hemelytral structure than any other group of Cimicomorpha, but in leptopodoids the costal fracture is arched, strongly inclined, ending not far from the apex of medial fracture, A1 remote from commissural margin, and membrane cells are larger and usually more numerous.

REMARKS. The vein dSc is weak and usually overlooked in Velocipedini and other Nabidae (figured and termed R_a by Kerzhner [1981: figs 24, 26]).

Darniopseini Becker-Migdisova, 1958, **stat.n.**

TYPE GENUS. *Darniopsis* Becker-Migdisova, 1958.

DIAGNOSIS. Small. Hemelytra 4–5 mm long. Cuneus elongate trapezoidal, with apical margin nearly straight, not prolonged along costal margin. Discal cells longer than 1/3 of basal cell. Composite vein separating discal and membrane cells slightly zigzagged, in cell 1 running within cuneus, and not coincident with straight, indistinct corium/membrane boundary. Live cells occupying no less than 1/3 of membrane, posterior ones longer than anterior. Membrane beyond live cells with few or no veins and no dead cells, sometimes with free posterior vein. Pcu arched backwards, remote from claval suture. Embolium subdivided near base. Corium and clavus with narrow veins and without deep punctures.

COMPOSITION. Type genus, *Juracipeda* **gen.n.,** and presumably also *Saldonabis* **gen.n.**

COMPARISON. Distinct from two other tribes in the live cells occupying no less than 1/3 of membrane, posterior of them being longer than anterior (hemelytral characters of living and fossil Velocipedinae are compared in the Table 1).

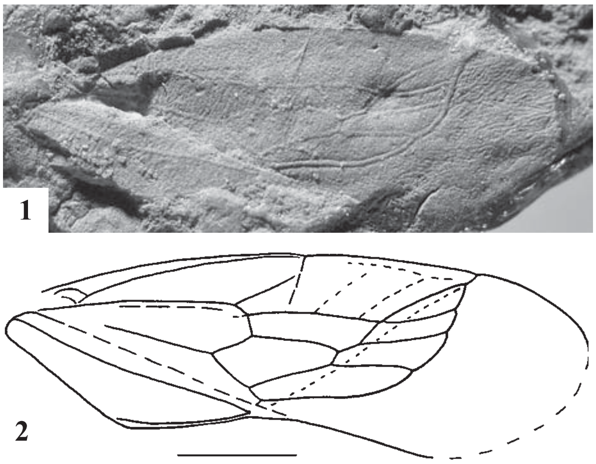
Darniopsis tragopea Becker-Migdisova, 1958
Figs 1–2.

MATERIAL. Holotype left hemelytron PIN no. 371/630 (part & counterpart) — Sogyuty, southern shore of Issyk-Kul Lake near Kadzhi-Say; Dzhil Formation, Lower Jurassic (Sinemurian?); coll. O.M. Martynova & Ya.M. Eglon, 1942.

DIAGNOSIS. Hemelytron 4.9 mm long. Costal margin convex. Live membrane cells small (cell 3 slightly shorther than discal cell 1), very unequal (cell 4 twice longer than cell 1 and much wider than cell 2). Discal cell 2 twice wider than discal cell 1. Corium/membrane boundary traceable by change in wing texture. Corium evenly sclerotized. Corium and clavus evenly, faintly punctate. Clavus ca. 0.43 hemelytron length. Membrane beyond live cells covered with

Table 1. Hemelytral and some other characters in Velocipedinae. Apomorphic states in **bold**.
Таблица 1. Признаки переднего крыла и другие признаки у Velocipedinae. Апоморфные состояния выделены **жирным**.

	Darniopseini			Vetantocorini	Velocipedini
	Saldonabis	*Darniopsis*	*Juracipeda*	*Izinabis* e.a.	*Scotomedes* e.a.
cuneus	elongate trapezoidal, not prolonged along costal margin				**sickle-shaped, prolonged**
discal cells	longer than 1/3 of basal cell				**<1/4 basal cell**
composite vein separating discal and membrane cells	zigzagged, in some places running on corium, not coincident with nearly straight, weak corium/membrane boundary				**~ straight, forming sharp corium/membrane boundary**
corial & claval veins	n a r r o w				**wide**
pronotal paranota	? retained			retained	**lost**
membrane cells	Large	~1/3 membrane		**narrow strip**	**<1/3 membrane**
posterior membrane cells	longer than anterior			**shorter than anterior**	
lengths of membrane cells	1<2<3<4	1<2<3<<4	1~2<3~4	**1~2>>3~4**	**1>2>3>4**
corium & clavus	evenly, faintly punctate			**smooth, pilose**	**deeply punctate**
membrane beyond live cells	?no veins	wrinkled	**4 blind veins from cells 1–2**	**dead cells & many veins**	**many veins, no dead cells**
costal margin	deeply convex		**shallowly convex**		deeply convex
membrane cell 1	~ closed	closed	**open**		~ closed **or open**
clavus length	~ 1/2 hemelytron		**< 1/2 hemelytron**		~ 1/2 hemelytron
discal cell 1	not narrow	**narrow**		not narrow	**narrow**
others (e.g. colour pattern)		cell 4 widest	posterior free vein	with pale-and-dark pattern	dark with pale spots



Figs 1–2. *Darniopsis tragopea* Becker-Migdisova, 1958 (Nabidae: Velocipedinae: Darniopseini), holotype PIN 371/630, Lower Jurassic, Dzhil Formation, Issyk-Kul, Kyrgyzstan: 1 — left hemelytron (mirrored); 2 — its venation. Scale bar 1 mm in all figures.

Рис. 1–2. *Darniopsis tragopea* Becker-Migdisova, 1958 (Nabidae: Velocipedinae: Darniopseini), голотип ПИН 371/630, нижняя юра, джильская свита, Иссык-Куль, Киргизия: 1 — левое переднее крыло (зеркально перевёрнуто); 2 — его жилкование. Масштабная линейка — 1 мм (здесь и далее на всех рисунках).

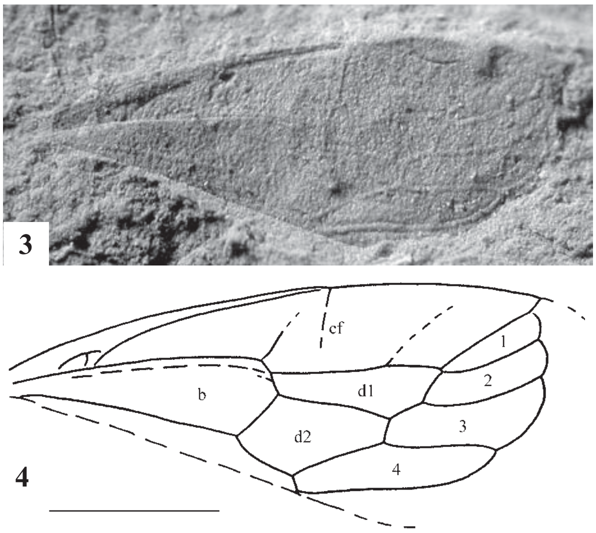
fine longitudinal and oblique wrinkles (some of them almost vein-like).

Saldonabis proteus Shcherbakov, **gen.** et **sp.n.**
Figs 3–4.

MATERIAL. Holotype right hemelytron PIN no. 358/1003 (part & counterpart) — Sogyuty, southern shore of Issyk-Kul Lake near Kadzhi-Say; Dzhil Formation, Lower Jurassic (Sinemurian?); coll. N.Ya. Kulik, 1928.

DIAGNOSIS. Hemelytron about 4 mm long (3.2 mm as preserved: clavus and membrane beyond cells missing). Costal margin convex. Live membrane cells large (cell 3 as long as discal cell 1), less unequal (cell 4 is 1.5 times longer than cell 1, and nearly not wider than cell 2), presumably occupying nearly 1/2 of membrane. Discal cell 2 is 1.5 times wider than discal cell 1. Corium/membrane boundary indistinct. Corium obscurely punctate. Cuneus along costal margin more sclerotized and apparently thickened.

COMPARISON. Distinct from the type genus in larger and less unequal membrane cells, and discal cell 1 not so narrow. The genus shows position of costal fracture characteristic of primitive Cimicomorpha. Nevertheless, it is similar to primitive Leptopodoidea in larger, subequal live membrane cells, and nearly no boundary between the corium and membrane, so it could stand nearer to leptopodoid ancestors than any other nabid group. The anteriorly thickened cuneus, that may play a role of pterostigma, is similar to analogous formations in other groups with poorly sclerotized corium: Ceresopseidae and other reduvioids (see below), some Miridae and Microphysidae, and some Gerromorpha (Hebridae, Mesoveliidae etc.). The course of A1 and degree of membrane development beyond cells, yet unknown in *Saldonabis* **gen.n.**, are important for elucidating its affinities. Venation of *Saldonabis* **gen.n.** resembles that in a hypothetical ancestor of Cimicomorpha as figured by Kerzhner [1981: fig. 98A]: saldid-like but with costal fracture more basal, straight and transverse.



Figs 3–4. *Saldonabis proteus* **gen.** et **sp.n.** (Nabidae: Velocipedinae: Darniopseini), holotype PIN 358/1003, Lower Jurassic, Dzhil Formation, Issyk-Kul, Kyrgyzstan: 3 — right hemelytron; 4 — its venation. Membrane cells numbered, d1–d2 — discal cells 1 and 2, b — basal cell, cf — costal fracture.

Рис. 3–4. *Saldonabis proteus* **gen.** et **sp.n.** (Nabidae: Velocipedinae: Darniopseini), голотип ПИН 358/1003, нижняя юра, джильская свита, Иссык-Куль, Киргизия: 3 — правое переднее крыло; 4 — его жилкование. Ячейки перепоночки пронумерованы, d1–d2 — дискальные ячейки 1 и 2, b — базальная ячейка, cf — костальный надлом.

ETYMOLOGY. From *Salda* and *Nabis;* gender masculine. In Greek mythology, Proteus is an early sea-god (his name suggests the 'first') who can foretell the future, but will change his shape to avoid having to, and only answer to someone who is capable of capturing him; 'protean' means 'capable of assuming many forms'.

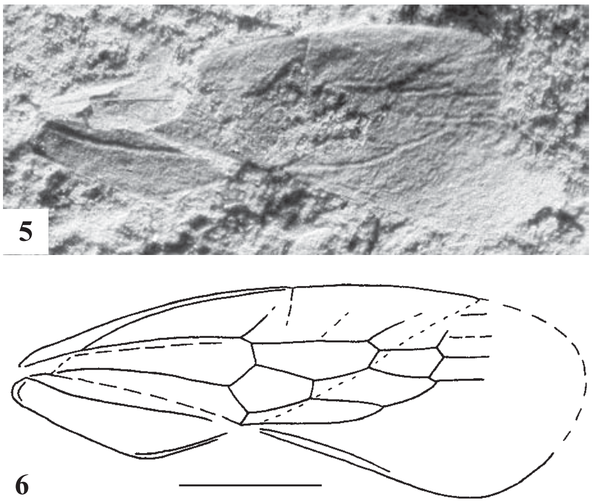
Juracipeda popovi Shcherbakov, **gen.** et **sp.n.**
Figs 5–6.

MATERIAL. Holotype right hemelytron PIN no. 923/770 (part & counterpart; outcrop 1/16) — right bank of Kempendyay River (tributary of Vilyui) below the mouth of Namdyr River, Suntar District, Yakutia; uppermost Jurassic (?); coll. I.D. Sukatsheva and other members of Arthropoda Lab, PIN, 1988.

DIAGNOSIS. Hemelytron about 4 mm long (3.8 mm as preserved: membrane incomplete), brown, gradually turning pale beyond live cells. Costal margin nearly straight. Live membrane cells small (cell 3 slightly shorther than discal cell 1), subequal cells 4 and 3 somewhat longer than cells 2 and 1. Discal cell 2 twice wider than discal cell 1. Corium/membrane boundary traceable. Corium and clavus impunctate. Membrane with two distinct free veins emanating from cell 2 and two indictinct ones from cell 1. Free vein very close to posterior margin of membrane, traceable up to distad of cell 4. Clavus ca. 0.42 hemelytron length.

COMPARISON. Distinct from two preceding genera in the costal margin shallowly convex, membrane cell 1 open, and clavus shorter than 1/2 hemelytron, being similar in these characters to the following tribe and possibly related to its ancestors.

ETYMOLOGY. From Jurassic and *Velocipeda;* gender feminine. The species is named after Dr Yu.A. Popov, the world authority in fossil Heteroptera and my friend, on the occasion of his 70th birthday.


5
6

Figs 5–6. *Juracipeda popovi* **gen.** et **sp.n.** (Nabidae: Velocipedinae: Darniopseini), holotype PIN 923/770, uppermost Jurassic (?), Kempendyay River, Yakutia: 5 — right hemelytron; 6 — its venation.

Рис. 5–6. *Juracipeda popovi* **gen.** et **sp.n.** (Nabidae: Velocipedinae: Darniopseini), голотип ПИН 923/770, верхи юры (?), р. Кемпендяй, Якутия: 5 — правое переднее крыло; 6 — его жилкование.

Vetanthocorini Yao, Cai et Ren, 2006, s.str.

TYPE GENUS. *Vetanthocoris* Yao, Cai et Ren, 2006

DIAGNOSIS. Small to medium-sized (6–13 mm long). Hemelytra 5.3–10 mm long, with costal margin shallowly convex to nearly straight (but nevertheless concealing sides of abdomen in repose), embolium wide to rather narrow. Cuneus elongate trapezoidal, with straight apical margin, not prolonged along costal margin. Discal cells longer than 1/3 of basal cell. Composite vein separating discal and membrane cells somewhat zigzagged, in cell 1 running within cuneus, and not coincident with straight, indistinct corium/membrane boundary. Live cells occupying narrow zone at base of membrane, posterior ones shorter than anterior, cell 1 narrowly open, stub (processus corial) short. Membrane beyond live cells with four dead veins, forming three cells surrounded by numerous radiating branches at the membrane periphery, several anteriormost of these branches parallel to corium/membrane boundary. Pcu arched backwards, remote from claval suture. Embolium not subdivided near base. (Details of venation known for *Izinabis*, **gen.n.**). Commissura clavi about as long as exposed part of mesonotum. Corium and clavus smooth, hairy, with narrow veins. Head short subconical, in dorsal aspect about as wide as long (including eyes, excluding neck). Ocelli situated at level of posterior margin of eyes. Rostrum long, highly movable (preserved in various position, often directed forwards), 3rd segment very long (longer than 2nd+4th). Antennae with 2nd segment very long (usually not shorter than 3+4th) and widened towards apex, 3–4th segments much thinner than 2nd, 4th segment shorter than or subequal to 3rd. Collar narrow, anterior lobe of pronotum not longer than posterior one, posterior margin shallowly emarginate, sides slightly convex, explanate (forming pronotal paranota). Legs long and slender, femora not incrassate. Mid and hind coxae cardinate (see [Yao et al., 2006: fig. 26]). Hind tibia longer than abdomen width, with long, thick, suberect setae; mid and fore tibiae with similar or weaker setae. Tarsi slender, 3-segmented, 1st segment short, triangular (see hind tarsus in [ibid.: fig. 16]), 3rd longest. Abdomen in both sexes with wide, clearly demarcated ventral laterotergites; 8th segment in male well developed, somewhat shorter than 7th. Male genitalia symmetrical. Female genitalia laciniate. Body mostly dark (at least pronotal paranota pale), 2nd antennal segment usually dark apically and pale at least medially; hemelytra with variegate colour pattern, sometimes pale with dark cuneus, if dark then clavus mostly pale.

COMPOSITION. *Vetanthocoris* Yao, Cai et Ren, 2006, *Collivetanthocoris* Yao, Cai et Ren, 2006, *Byssoidecerus* Yao, Cai et Ren, 2006, and *Mecopodus* Yao, Cai et Ren, 2006 from the Early Cretaceous Yixian Formation, Liaoning, China; *Izinabis*, **gen.n.** from the Early Cretaceous of eastern Mongolia; possibly also *Mesanthocoris* Hong et Wang, 1990 from the Early Cretaceous Laiyang Formation, Shandong, China (*Liaoxia* Hong, 1987 and *Curvicaudus* Yao, Cai et Ren, 2006 not included, see Remarks).

COMPARISON. Vetanthocorini s.str. are distinct from Anthocoridae s.l. and similar to Nabidae s.l., especially Velocipedini, in the rich membrane venation including live cells, symmetrical male genitalia, strong setation of tibiae, and larger size (anthocorids are up to 6 mm long), therefore this tribe is transferred from Anthocoridae s.l. to Nabidae s.l. (very long 3rd rostral and 2nd antennal segment are found in both Velocipedini and some Anthocoridae s.l., e.g. Eocene Lyctoferini [Popov, 2003]).

Vetanthocorini s.str. are distinct from Darniopseini and Velocipedini in the narrow strip of live cells (posterior ones shorter than anterior) plus several dead cells and numerous dead veins (anterior ones oblique) in the membrane, and from Velocipedini in the head shorter, sides of pronotum explanate, and pale pattern of hemelytra more extensive. Similar to Velocipedini (see below) in the 2nd antennal segment very long and lateral setation of tibiae (some Prostemmatini and Nabini also have these setae well developed but shorter and either thicker or more adpressed).

Vetanthocorini s.str. are similar to Medocostinae, Prostemmatinae, and Nabinae in live venation of membrane greatly reduced, but distinct from these three subfamilies in the small live cells retained in membrane (along with dead venation), from Medocostinae in the sides of abdomen concealed in repose, from Prostemmatinae in the shorter anterior pronotal lobe, from Medocostinae and Prostemmatinae in the complete venation of corium, and from Medocostinae and Nabinae in the presence of long costal fracture (short costal fracture retained in macropterous and some brachypterous specimens of *Prostemma* Laporte, 1832 [Kerzhner, 1981]).

REMARKS. Six genera and seven species were originally assigned to this tribe. Of them, *Liaoxia longa* Hong, 1987, as characterized by Yao et al. [2006], does not belong in Velocipedinae on account of 3rd antennal segment and 4th rostral segment longest (in the latter character similar to Medocostinae).

Another monobasic genus, *Curvicaudus* is distinct from the type genus in three important characters: 3–4th antennal segments almost as thick as 2nd; pale pronotal paranota either undeveloped or much narrower than in other genera; male pregenital abdomen (and presumably genitalia) asymmetrical (in the only male known, paratype CNU-HE-LB2006024 of *C. ciliatus* [Yao et al., 2006: fig. 45] the hind margin of 7th and whole 8th abdominal segment look somewhat S-shaped; the holotype of this species reported as another male is in fact female, as judged from its broader abdomen with one fully development segment less and triangular apex [ibid.: fig. 44]). Rich membrane venation characteristic of typical Vetanthocorini is not reported in *C. ciliatus;* its body length ca 7.5

mm, length of hemelytron ca. 6.3 mm (anthocorids are up to 6 mm long). On the other hand, this genus is similar to *Vetanthocoris* in many other characters, including the shape and even colour pattern of the 2nd antennal segment. It is quite possible that *Curvicaudus* showing anthocorid traits indeed belongs to the most primitive Anthocoridae s.l., documenting the origin of these latter from Velocipedinae s.l.

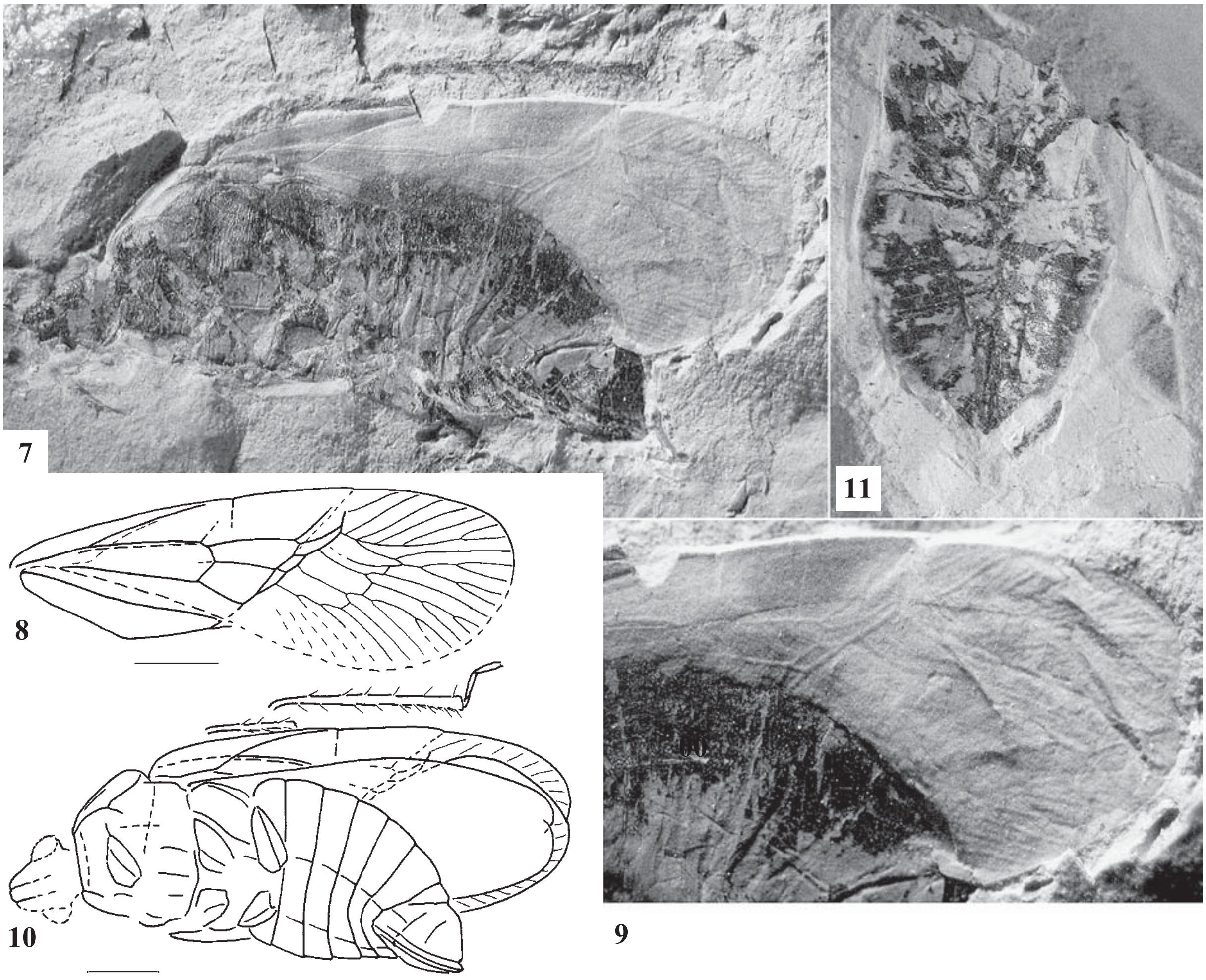
Some characters used as diagnostic by Yao et al. [2006] are either artifacts of preservation (length of abdomen relative to tips of folded hemelytra varies greatly depending on postmortal extension) or need reconsideration (paired pale lines interpreted as pronotal carinae or sulci in *Curvicaudus* are rather membranous parapsidal clefts of mesonotum visible through pale posterior pronotal lobe); some other important characters were overlooked (well developed costal fracture — see [ibid.: fig. 5]; live cells of membrane — their distal boundary figured as straight line parallel to corium/membrane boundary [ibid.: fig. 3])

One more fossil from the Early Cretaceous (see below) Laiyang Formation, China, *Mesanthocoris brunneus* Hong et Wang, 1990 (12 mm long, hemelytron 7 mm), similar to Vetanthocorini in the structure and even colour pattern of antenna, strong tibial setae, and size, needs re-examination: rostrum as figured seems disproportionally short (may be incompletely preserved); sides of pronotum looking nearly straight may bear pale paranota. The genus assigned to Anthocoridae in the Chinese text of the paper was erroneously indicated as belonging to Mesanthocoridae (neither marked as fam.n. nor supplied with diagnostic characters) in the extensive English summary [Hong & Wang, 1990: 177].

Another fossil from the same formation, *Mesopyrrhocoris fasciata* Hong et Wang, 1990 (6.8 mm long, hemelytron 4 mm) with similar antennae and very distinctive dark pattern (numerous veins figured on membrane are not visible in the photograph), described in Pyrrhocoridae, should be transferred to Cimicomorpha, but its more precise affiliation remains unknown due to insufficient preservation.

Izinabis kerzhneri Shcherbakov, **gen.** et **sp.n.**
Figs 7–11.

MATERIAL. Holotype female PIN no. 3965/337 (part & counterpart, antennae and rostrum not preserved; outcrop 300/1) and paratype female PIN no. 3965/433 (part & counterpart, head and prothorax missing; outcrop 334/1) — southern slopes of Hutel-Hara Mt. 70 km SE Sain Shand, East Gobi Aymag,



Figs 7–11. *Izinabis kerzhneri* **gen.** et **sp.n.** (Nabidae: Velocipedinae: Vetanthocorini), Tsagaan-Tsav Formation, Lower Cretaceous, Hutel-Hara Mt., Mongolia: 7–10 — holotype female PIN 3965/337: 7, 10 — habitus, lateroventral view; 8 — venation of hemelytron; 9 — part of left hemelytron (mirrored; note live cells of membrane; 11 — paratype female PIN 3965/433, habitus.

Рис. 7–11. *Izinabis kerzhneri* **gen.** et **sp.n.** (Nabidae: Velocipedinae: Vetanthocorini), цаганцабская свита, нижний мел, Хутэл-Хара, Монголия: 7–10 — самка, голотип ПИН 3965/337: 7, 10 — общий вид снизу-сбоку; 8 — жилкование переднего крыла; 9 — часть левого переднего крыла (зеркально перевёрнуто; видны живые ячейки перепоночки); 11 — самка, паратип ПИН 3965/433, общий вид.

Mongolia; lower Tsagaan-Tsav Formation, Lower Cretaceous; coll. S.M. Sinitza, A.G. Ponomarenko, and other members of Arthropoda Lab, PIN, 1980.

DIAGNOSIS. Body with folded hemelytra 7.9 mm long, hemelytron 5.9 mm long (holotype female). Costal margin shallowly convex; embolium not much widened towards base (about 10 times as long as wide). Discal cell 2 not much wider than discal cell 1. Membrane with live cells occupying very narrow zone at its base (posterior ones at least thrice shorter than anterior) plus dead venation: four veins emanating from live cells 2–4 and numerous fanning branches at membrane periphery. Clavus ca. 0.45 hemelytron length. Body and legs dark, pronotum with at least paranota pale, hemelytra pale with cuneus mostly dark (except base); pubescence short, sparse, black. Structure of antennae and rostrum unknown.

COMPARISON. Distinct from *Vetanthocoris*, *Collivetanthocoris*, and *Byssoidecerus* in narrower embolium and hemelytra pale except for cuneus, from poorly known *Mecopodus* in the more developed tibial setation and larger size, from *Mesanthocoris* and *Curvicaudus* in much broader, pale pronotal paranota, and from the latter also in the more extensive dark spot in cuneus.

ETYMOLOGY. The genus and species are named after Dr Iz. M. Kerzhner, the head of Russian heteropterists. Gender masculine.

Velocipedini Bergroth, 1891

DIAGNOSIS (only characters relevant to present discussion). Small to medium-sized (6–13 mm long), sometimes subbrachypterous. Hemelytra 4–9 mm long, with costal margin deeply convex, embolium explanate. Cuneus sickle-shaped, short but prolonged along costal margin. Discal cells shorter than 1/4 of basal cell. Composite vein separating discal and membrane cells nearly straight, forming distinct corium/membrane boundary. Live cells occupying less than 1/3 of membrane, posterior ones shorter than anterior, cell 1 open (stub short) or closed by dead vein continuing the stub. Membrane beyond live cells with 10–12 longitudinal dead veins not forming few dead cells, anterior of these veins not parallel to corium/membrane boundary. Pcu slightly arched backwards or nearly straight. Commissura clavi about as long as exposed part of mesoscutum. Corium and clavus deeply punctate, with wide veins margined with punctures. Clavus 0.42–0.48 (in subbrachypters up to 0.58) hemelytron length. Head long subconical, in dorsal aspect much longer than wide (including eyes, excluding neck). Ocelli situated at level of posterior margin of eyes. Rostrum very long (at least reaching middle coxae), highly movable, 3rd segment extremely long. Antennae with 2nd segment very long (sometimes as long as 3+4th) and widened towards apex, 3–4th segments very thin, 4th shorter than 3rd. Collar narrow, anterior lobe of pronotum shorter than posterior one, posterior margin emarginate, sides ridged, nearly straight to sinuate. Legs long and slender, femora not incrassate. Hind coxae subcardinate. Hind tibia longer than abdomen width, with stiff, suberect setae; setation of mid and fore tibia less developed (see Remarks). Tarsi slender, 3-segmented, 1st segment short, triangular, 3rd longest. Abdomen with narrower, feebly demarcated ventral laterotergites in male only; 8th segment in male well developed, as long as 7th. Male genitalia symmetrical. Female genitalia laciniate. Dark coloured, hemelytron usually with one–three pale spots along costal margin (second and third at base and apex of cuneus, respectively), clavus dark.

COMPOSITION. Three extant genera.

COMPARISON. Distinct from two other tribes in the sickle-shaped cuneus, short discal cells, nearly straight vein separating discal and membrane cells, corium and clavus deeply punctate, with wide veins, and also from Vetanthocorini in the head longer, sides of pronotum not explanate, and hemelytra mostly dark.

REMARKS. Hind tibiae in modern Velocipedini bear thin, stiff, suberect, brown setae about as long as diameter of the tibia (rarely longer), arranged in four irregular rows, 10–12 setae in each row; there are only two rows of 7–8 shorter setae on the middle, and a single row of 7–8 setae on the fore tibiae, as observed by D.A. Gapon (pers. comm.) in *Scotomedes alienus* (Distant, 1904) and *Costomedes morobensis* Doesburg, 2004 kept in Zoological Institute, St.-Petersburg.

Reduvioidea Latreille, 1807

Ceresopseidae Becker-Migdisova, 1958

TYPE GENUS. *Ceresopsis* Becker-Migdisova, 1958.

DIAGNOSIS (Figs 12–15). Small. Hemelytra 4.5–5.5 mm long, with costal area wide, more than 1/3 width of hemelytron, costal margin convex. Embolium wide and not subdivided near base. R with weak anterior branch (dSc) basal to costal fracture. Corium with rather narrow basal cell and two discal ones about 1/2 of basal cell. Three large, broad live cells (2–4) in basal half of membrane (cell 3 distinctly longer than discal cell 1), sometimes rudimentary anterior cell 1 present, closed distally, but poorly separated from cell 2 (Fig. 12). Costal fracture arched, oblique, in basal 1/2 hemelytron, ending close to apex of basal cell and apex of medial fracture (Fig. 14). Membrane cells occupying about 1/2 membrane length; cell 3 largest, extended distad of cells 2 and 4; two–three blind veins emanating from cells 2, 4 and

Table 2. Hemelytral characters of Darniopseini and *Ceresopsis*.
Таблица 2. Признаки переднего крыла Darniopseini и *Ceresopsis*.

	Darniopseini	*Ceresopsis*
costal fracture	straight, subtransverse, ~ 1/2 hemelytron, ending not close to apex of medial fracture	arched, oblique, in basal 1/2 hemelytron, ending close to apex of medial fracture
embolium nr. base	subdivided by arched lines	not subdivided
membrane cells	< 1/2 membrane length (?*Saldonabis*)	~ 1/2 membrane length
membrane cell 1	full-sized, closed or open	rudimentary (closed) or absent
membrane cell 3	not largest, level with cells 2 & 4	largest, extended distad of cells 2 & 4
blind veins beyond cells	no or four from cells 1–2	two–three from cells 2, 4 and sometimes 3
corium	well sclerotized, with veins less distinct than at base of membrane	little sclerotized except in embolium and cuneus, veins as distinct as on membrane

sometimes 3; free posterior vein absent. Corium and membrane of very similar texture, with distinct veins, those on membrane margined with grooves and therefore appear wider, more depressed and less clearly cut than raised veins on corium; the corium/membrane boundary traceable only due to this change in vein structure and position (Fig. 15). Base of embolium and anterior half of cuneus more sclerotized and apparently thickened. Corium indistinctly sparsely granulate; membrane covered with faint oblique and irregular wrinkles. Clavus ca. 0.4 hemelytron length (its structure unknown).

COMPOSITION. Type genus with three species described, all from Sogyuty, Kyrgyzstan; Dzhil Formation, Lower Jurassic.

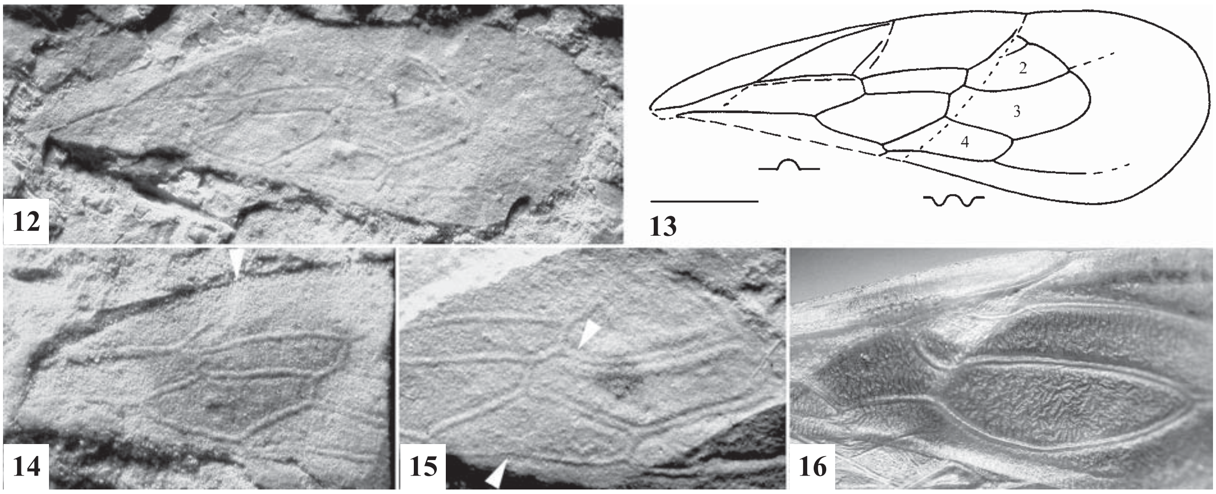
COMPARISON. Quite similar to Darniopseini in the basic venation pattern, but differ in the less sclerotized corium, the shape, size and basic number of membrane cells and of blind veins emanating from them, and the shape and position of costal fracture (see Table 2). In these characters (except for costal fracture) similar to Reduviidae s.l.: reduviids usually show corium poorly sclerotized (often more so in cuneal region) with veins raised and membrane with veins similar but margined by grooves and thus depressed (Fig. 16). Distinct from Reduviidae in the retention of costal fracture, much broader costal area, and membrane cells reaching only half membrane length. In the larger live membrane cells, ill-defined boundary between the corium and membrane, and cuneus thickened anteriorly more similar to primitive Leptopodoidea than Darniopseini other than *Saldonabis* **gen.n**.

REMARKS. The costal fracture is best preserved in the holotype of *C. ornata* Becker-Migdisova, 1962; the costal area detached along costal and medial fractures is missing in the holotype of *C. vitrea* Becker-Migdisova, 1962.

On the phylogeny of Cimicomorpha

Cladistics denies paraphyletic (= ancestral) groups as unnatural and not legitimate, and admits only holophyletic (= monophyletic s.str. = terminal) ones; an alternative, more fossil-friendly approach named ‘phylistics’ by Rasnitsyn [1996] welcomes the taxa of both categories. Cladistic systematics requires splitting paraphyletic assemblages (such as Nabidae s.l. or Anthocoridae s.l.) into holophyletic units according to sequenced apomorphies. Phylistics, like practical taxonomy, subdivides taxonomic continuum according to hierarchy of gaps between groups, and taxonomists still do not follow the cladistic recommendations to split Nabidae s.l. and Anthocoridae s.l. (see e.g. Aukema & Rieger [1996]).

The phylogenetic diagram of Cimicomorpha by Kerzhner [1981: fig. 97] and the cladogram by Schuh & Štys [1991: fig. 1] agree that Cimicoidea s.str. branch off (possibly as two clades, Plokiophilidae and the rest) from the lineage of Nabidae s.l. (Velocipedini–Nabinae) between Velocipedini and Medocostinae, and that Joppeicidae, Thaumastocoridae, Vianaididae and Tingidae belong to the same major lineage. According to Kerzhner [1981], Reduvioidea branch off from nabid lineage after Medocostinae, Microphysidae and Miridae form a sister lineage to Cimicoidea s.l. + Reduvioidea, and these two lineages together are opposed to joppeicid-tingid one. On the contrary, according to Schuh & Štys [1991], Reduvioidea form the most basal lineage in Cimicomorpha (mentioned as a possible alternative by Kerzhner [1981: 74]), Miriformes s.l. (Microphysidae, Miridae,



Figs 12–16. Ceresopseidae (Reduvioidea; Lower Jurassic, Dzhil Formation, Sogyuty, Kyrgyzstan) and Reduviidae (recent): 12–13 — *Ceresopsis costalis* Becker-Migdisova, 1958, holotype PIN 371/570: 12 — right hemelytron; 13 — its venation (with schematic cross-sections of corium and membrane veins, membrane cells numbered); 14 — *C. ornata* Becker-Migdisova, 1962, holotype PIN 358/487, left hemelytron (mirrored; costal fracture marked with arrow); 15 — *Ceresopsis* sp., PIN 457/43, part of left hemelytron (mirrored) near corium/membrane boundary (arrows; note difference in the structure of their veins); 16 — *Stirogaster fausti* Jakovlev, 1874 (Reduviidae Stenopodainae), same as on Fig. 15 (note thickened cuneal region).

Рис. 12–16. Ceresopseidae (Reduvioidea; нижняя юра, джильская свита, Согюты, Киргизия) и Reduviidae (современный): 12–13 — *Ceresopsis costalis* Becker-Migdisova, 1958, голотип ПИН 371/570: 12 — правое переднее крыло; 13 — его жилкование (со схематическими поперечными срезами жилок кориума и перепоночки, ячейки перепоночки пронумерованы); 14 — *C. ornata* Becker-Migdisova, 1962, голотип ПИН 358/487, левое переднее крыло (зеркально перевёрнуто; костальный надлом показан стрелкой); 15 — *Ceresopsis* sp., PIN 457/43, часть левого переднего крыла (зеркально перевёрнуто) около границы кориума и перепоночки (показана стрелками; заметна разница в строении их жилок); 16 — *Stirogaster fausti* Jakovlev, 1874 (Reduviidae Stenopodainae), современный, то же что на рис. 15 (виден утолщённый район кунеуса).

Thaumastocoridae and Tingidae s.l., including Vianaidinae) branch off from nabid stem after Velocipedinae, and Miridae rather than Thaumastocoridae are closest relatives of Tingidae.

Recently described Early Cretaceous Ignotingidae show the same set of apomorphic traits as Tingidae s.str. (areolation, hypertrophied pronotum with median crest, basic structure and venation pattern of hemelytron, very long antennae and legs, shortened tarsi, rotatory hind coxae), combined with several important plesiomorphies not found in Vianaididae and Tingidae s.str. (vertical head without prominent bucculae or other projections, thick rostrum not appressed to venter, no thoracic sternal laminae, three-segmented tarsi, laciniate ovipositor not concealed by paratergites) or even in the Miridae and Tingidae s.l. (small fossula spongiosa) [Zhang et al., 2005]. The Laiyang Formation yielding *Ignotingis* (and *Mesanthocoris*) is apparently of earliest Cretaceous age, according to composition of its insect assemblage rich in aphids. The tibial appendix of Thaumastocorinae was considered not homologous to fossula spongiosa by Kerzhner [1981] and Schuh & Štys [1991], but its setae are modified (illustrated in Schuh & Slater [1995: fig. 52.3D]), not simple (as stated by Kerzhner [1981]), therefore we regard that fossula spongiosa is retained in some Miriformes sensu Schuh & Štys (Thaumastocorinae, Ignotingidae) [Zhang et al., 2005]. *Ignotingis* Zhang, Golub, Popov et Shcherbakov, 2005 confirms the hypothesis on the origin of Tingidae s.l. from primitive mirid-like ancestors [Péricart, 1983] which still retained symmetrical genitalia and fossula spongiosa [Zhang et al., 2005] rather than from thaumastocorid-like forms. The fossula spongiosa apparently belongs to the groundplan of the Cimicomorpha.

Based on hemelytral venation of *Ignotingis,* the live membrane cells 1–4 were apparently incorporated into the corium in Tingidae, the cell 1 forming the apex of 'subcostal' (in fact, costal) area, so the zone of tingid hemelytral overlap corresponds only to the posterodistal part of membrane in other Cimicomorpha [Zhang et al., 2005]. Slight difference in the position of corium/membrane boundary relative to the cell boundaries in Darniopseini+Vetanthocorini and Velocipedini provides further evidence that this position is not the same across Heteroptera.

Darniopseini and Vetanthocorini as characterized above strengthen Kerzhner's concept of Nabidae s.l. as the stem lineage of at least Cimicoidea s.l.

Ceresopseidae are quite similar to Darniopseini in the basic venation pattern, but demonstrate several important differences (listed in the Table 2). Five of these seven features (shape, size and basic number of membrane cells and of blind veins emanating from them, and sclerotization of corium) correspond to the venational differences between Reduviidae s.l. and Nabidae s.l. One more difference (shape and position of costal fracture) may likewise be interpreted in that way: the straight, subtransverse, distally displaced costal fracture is found in Cimicoidea s.l. and Microphysidae + Miridae, whereas no remnant of costal fracture was ever recorded in any Reduviidae (as well as in Joppeicidae and Tingoidea). In the arched, oblique costal fracture nearly touching the apex of medial fracture, Ceresopseidae are similar to leptopodoid ancestors rather than to Darniopseini, but the latter are more primitive in retaining four less unequal membrane cells and embolium subdivided near base. Two or three blind veins emanating from the cells 2–4 in *Ceresopsis* strikingly resemble those of Reduviidae. Two blind veins from the cells 2 & 4 are found also in Early Jurassic Gerromorpha (*Engynabis* Bode, 1953, *Sphongophoriella* Becker-Migdisova, 1958), but these latter differ from Ceresopseidae and Reduviidae in the middle membrane cell (cell 3) small, and both costal and claval areas greatly diminished. These earliest gerromorphans co-occurring with *Ceresopsis* were already much more advanced than the latter, implying that evolution of surface bugs followed another line of descent. In some Reduviidae (e.g. *Lisarda*, Stål 1859) and Gerromorpha two arched blind veins tend to meet each other, nearly closing a distal cell in membrane. The blind veins probably represent remnants of the distal membrane cell series found in Nepomorpha (otherwise this similarity of Ceresopseidae + Reduviidae and Gerromorpha should be interpreted as homoplastic). Presumably the series of dead cells in Nabidae (arranged distad of the live cell series) is also homologous to this distal cell series of the earliest bugs. If so, then reduction of membrane venation, with or without loss of tracheae and nerves in the veins ('vein death'), proceeded along similar ways, but differed in details in Reduvioidea, other Cimicomorpha, and more distantly related bugs (e.g. Gerromorpha), first affecting the distal cell series and then proximal one.

Ceresopseidae differ from Reduviidae in retention of costal fracture, much broader costal area, and membrane cells reaching only half membrane length; the latter character indicates that these cells became secondarily expanded in extant reduviids. Ceresopseidae are herein placed in Reduvioidea as plausible ancestors of Reduviidae. This casts some doubt on pachynomid-reduviid relationship, already questioned by Cobben [1968: 356], the more so that Stål [1873] and other authors placed Pachynomidae close to Nabidae. Indeed, at the first glance hemelytra of Pachynomidae look similar to those of Nabidae s.str. rather than Ceresopseidae and Reduviidae: corium markedly sclerotized, well differentiated from membrane; costal fracture (retained in *Pachynomus* Klug, 1830) transverse, rather distal (at 2/3 of corium length = at level of claval apex). However, further characters reveal the above similarity is superficial: (i) basal cell reaching corium/membrane boundary, discal cells lost, R leaving basal cell proximally and running along costal margin (condition uncommon in Cimicomorpha, but usual in Pentatomomorpha); in *Pachynomus,* (ii) medial fracture is extended beyond costal fracture and the level of claval apex [Carayon & Villiers, 1968: pl. IB], and (iii) veins delimiting three long membrane cells are wide, margined with grooves, dissimilar to narrow, groove-like fanning peripheral branches (whereas in Nabidae s.str. veins delimiting dead membrane cells and peripheral branches are of the

same structure). Therefore, (i–ii) the costal fracture in *Pachynomus,* though rather distal, is nevertheless proximal to the apex of hypertrophied basal cell, therefore being more similar to the condition found in Ceresopseidae (costal fracture almost reaching apex of basal cell) than to that of Cimicoidea s.l. etc. (more distal, remote from apex of basal cell), and (iii) the membrane cells in Pachynomidae are less reduced, probably more similar to the live cells than to the dead ones. This limited evidence agrees with the idea of Carayon [1950] who united Pachynomidae with Reduviidae. Pachynomids probably separated early from reduvioid stem and acquired some homoplastic similarities to cimicoids.

Retention of the 1st abdominal spiracle in adults of Reduviidae and Pachynomidae (like in Nepo-, Gerro-, and Leptopodomorpha) is likely a plesiomorphy. Old authors reported this spiracle also in some Nabidae, Cimicidae and Miridae, and its scar was found in nymphal Anthocoridae [see Cobben, 1968]. This spiracle is undeveloped in adults of remaining Cimicomorpha (apomorphy 27-1 in Schuh & Štys [1991]). Alternatively, it may be an apomorphy, more exactly, a reversal to the plesiomorphic state (susceptible to homoplasy) through retention of the nymphal condition at the adult stage, probably due to loss of hemelytra-body coaptation at the thoraco-abdominal junction.

Antennae of 'velocipedine' type, with 2nd segment (pedicel) very long and 3–4th segments shorter and much thinner, seem to be very common in Mesozoic Cimicomorpha. Similar structure of antennae found also in Medocostinae, some Anthocoridae s.l., and Reduviidae is probably primitive for the infraorder. Sides of pronotum expanded into paranota are primitive at least for Hemiptera, were characteristic of early Heteroptera, and retained in Nepomorpha, Leptopodomorpha, Vetanthocorini (and presumably Darniopseini) and many groups of Cimicomorpha.

Several phylogenetically important characters of family-group taxa in Cimicomorpha are summarized in the Table 3.

Table 3. Selected phylogenetically important characters of the family-group taxa in Cimicomorpha.
Таблица 3. Некоторые филогенетически важные признаки таксонов группы семейства в Cimicomorpha.

apomorphic state	Ceresopseidae	Reduviidae s.l.	Pachynomidae	Darniopseini + Vetanthocorini + Velocipedini	Medocostinae	Prostemmatinae + Nabinae	Cimicoidea s.str.	Microphysidae	Miridae	Joppeicidae	Thaumastocoridae	Ignotingidae	Vianaididae + Tingidae s.str.
head trichobothria lost	0?[1]	0	0	0?[1]	0	0	01	0	1	1	1	1	1
pedicel trichobothria lost	0?[1]	0	0	01[2]	1	1	1	1	1	1	1	1	1
pedicel short	0?[1]	0	0	0	0	0	0	0	0	1	01	0	01
fossula spongiosa lost	0?[1]	01	0	0?[1]1	0	0	0	1	1	1	01	0?	1
costal fracture lost	0	1	01	0	1	01	0	0	0	1	1	1	1
live membrane cells lost	0	0	0	0	1	1	1	0	0	1	1	1[3]	1[3]
stub (processus corial) present	0	0	0	01	1	1	1	1	1	0	0	0[3]	0[3]
hind coxae rotatory	0?[1]	01	1	0	0	0	0	0	0	1	1	1	1
less than 3 tarsal segments	0?[1]	01	0	0	0	01	01	1	01	1	1	0	1
abdominal spiracle 1 absent	0?[1]	01	0	0?[1]1	1	0?[4]1	0?[4]1	1	0?[4]1	1	0	1	1
male abdom. segment 8 reduced	0?[1]	1	1	0	1	01	0	0	0	0	0	0	0
parameres asymmetrical	0?[1]	01	0	0	0	01	01	0	1	0	1	0	0
parameres directed caudad	0?[1]	1	1	0?[1]	0	01	01	0	1	0	0	1	1
female genital apophysis lost	0?[1]	1	0	0?[1]	0	0	01	1	1	1	1	1	1
ovipositor platelike or reduced	0?[1]	1	1	0	0	01	01	0	0	1	1	0	0

Classification mainly after Kerzhner [1981]. Character states based on Cobben [1968], Kerzhner [1981], Schuh & Štys [1991], Zhang et al. [2005]: 0 — plesiomorphic, 1 — apomorphic , 01 — variable (both apomorphic and plesiomorphic states found within the taxon).
[1] unknown for Ceresopseidae, Darniopseini and Vetanthocorini
[2] one trichobothria in *Scotomedes* and *Bloeteomedes* Doesburg, 1970, no one in *Costomedes* Doesburg, 2004 [Doesburg, 2004]
[3] live cells and stub vein incorporated into the corium in Tingoidea [Zhang et al., 2005]
[4] reported as present in some members [Handlirsch, 1899; Mammen, 1912 — both cit. after Cobben, 1968]

Классификация в основном по Кержнеру [1981]. Состояния признаков по Cobben [1968], Кержнеру [1981], Schuh & Štys [1991], Zhang et al. [2005]: 0 — плезиоморфное, 1 — апоморфное, 01 — варьирующее (и апоморфное, и плезиоморфное состояние встречается в таксоне).
[1] неизвестно для Ceresopseidae, Darniopseini и Vetanthocorini
[2] одна трихоботрия у *Scotomedes* и *Bloeteomedes* Doesburg, 1970, ни одной — у *Costomedes* Doesburg, 2004 [Doesburg, 2004]
[3] живые ячейки и слепая жилка вошли в состав кориума у Tingoidea [Zhang et al., 2005]
[4] отмечено у некоторых представителей [Handlirsch, 1899; Mammen, 1912 — цитируются по Cobben, 1968]

As first proposed by Handlirsch [1906–1908] (based on comparative morphology and fossils), water bugs (Hydrocorisae Latreille, 1802 = Cryptocerata Fieber, 1851 = Nepomorpha Popov, 1968) constitute the earliest radiation within Heteroptera. One hundred years later, this view still holds true, despite accumulation of much more extensive data on the fossil true bugs. No Heteroptera exist in the Permian, and all described Triassic forms are attributable to extinct or extant families of Nepomorpha, whereas the first land and surface bugs, represented with at least six superfamilies, are recorded in the Early Jurassic (coreoid s.l. Pachymeridiidae in the terminal Triassic, indistinguishable from basal Jurassic in the insect fauna) [Shcherbakov & Popov, 2002]. Therefore the latest version of phylogeny including fossil lineages [ibid.: fig. 179] is surprisingly similar to Handlirsch's tree.

Ceresopseidae formerly regarded by us as Heteroptera incertae infraordinis, possibly ancestral to Gerromorpha [ibid.: 148], are placed in Reduvioidea herein. The occurrence of both Cimicioidea s.l. and Reduvioidea in one of the earliest faunas containing non-nepomorphan bugs, makes the opinion on polyphyly of Cimicomorpha [Cobben, 1968] more probable.

Some species of Late Mesozoic Vetanthocorini are rather common as fossils (the type series of *Vetanthocoris decorus* Yao, Cai et Ren, 2006 includes about 40 specimens), so these bugs presumably lived near lake shores and used their long rostra for probing some substrate — the lifestyle not far from one hypothesized for ancestral heteropterans [Shcherbakov & Popov, 2002]. Tibial setation of Vetanthocorini similar to that of Velocipedini and Saldidae indicates that they were agile bugs possibly able to jump. Their contrasting colour pattern resembles that of such saldids as *Pentacora* Reuter, 1912 more than that of some anthocorids (though pale 2nd antennal segment with dark apex is found rather in the latter group), and might be used for signalling, implying open mode of life. Similar lifestyle is probable also of *Ceresopsis* spp., constituting more than a half of heteropteran specimens in the Early Jurassic of Sogyuty. Such mode of life is likely to be retained in some degree in the most primitive living Nabidae s.l., Velocipedini that are possibly confined to loose, wet substrates rich in invertebrate prey [Kerzhner, 1981: 70]. *Medocostes* Štys, 1967 has the rostrum very long, similar to Velocipedini (but with 4th segment longest), is likewise found in wet situations, and presumably feeds on subcorticolous insects (collected near the stream on dead trees [Kerzhner, 1989]).

The fossils discussed above indicate that:

– in Reduviidae well-developed membrane cells 2–4 (cell 1 is lost or merged with cell 2, as evidenced by Ceresopseidae) are homologous to corresponding live cells of Velocipedinae and other Cimicomorpha, in Tingoidea the cells 1–4 are incorporated into the corium s.l., whereas in most Cimicoidea s.l. the cell 1 is open, the vein delimiting it reduced to a stub (sensory processus corial), and the cells 2–4 become replaced with dead venation; no stub was ever developed in Reduvioidea;
– Pachynomidae probably represent an early branch of Reduvioidea;
– lineages of Ceresopseidae–Reduviidae s.l. and Darniopseini–Cimicoidea s.l. are traceable back to the earliest Jurassic, almost to leptopodoid ancestors;
– Nabidae s.str and Anthocoridae s.l. descended from the same group, Vetanthocorini, herein assigned to Velocipedinae s.l. in Nabidae s.l.;
– there is no evidence that the earliest Cimicomorpha belong to a single phyletic lineage; instead, reduvioid, cimicoid and possibly also miroid+tingoid lineages may well represent the closely related but different lines of ascent from primitive leptopodoid-like forms;
– ancestral Cimicoidea s.l. and Reduvioidea inhabited wet biotopes not far from the lakes.

Fossil record of Cimicomorpha

Available fossil record of cimicomorphan families is as follows [Shcherbakov & Popov, 2002; Popov, 2004; Yu.A. Popov, pers.comm.]:

– Velocipedinae (extinct Darniopseini) and extinct Ceresopseidae are first recorded in the Earliest Jurassic;
– Miridae (Orthotylinae and Mirinae) in the Late Jurassic [Herczek & Popov, 2001] (Middle Jurassic *Mirivena* Yao, Cai et Ren, 2007 shows very wide embolium, with C misinterpreted as R, and does not belong to the family);
– Tingidae, Reduviidae, Anthocoridae, and extinct Vetanthocorini, Ignotingidae and Golmoniini (Thaumastocoridae? Tingidae?) in the Early Cretaceous (Middle Jurassic *Hebeicoris luanpingensis* Hong 1983 transferred to Anthocoridae s.l. by Popov [1990] is correctly removed from this family by Yao et al. [2006]);
– extinct Ebboidae [Perrichot et al., 2006] (described in Tingoidea, but possibly related to Microphysidae — I.M. Kerzhner, pers.comm.) in mid-Cretaceous;
– Thaumastocoridae and Vianaididae in the Late Cretaceous;
– Microphysidae, Plokiophilidae and Nabinae in the Eocene; the oldest known Nabinae, *Metatropiphorus succini* (Jordan, 1952) from the Late Eocene Baltic amber (40–35 Ma) belongs to the genus considered the most primitive in this subfamily [Kerzhner, 1981].

Early Jurassic Pterocimicidae described as Cimicomorpha inc. superfam. [Popov et al., 1994] are herein transferred to Nepomorpha on account of their large, convex postclypeus bearing parallel muscle impressions (pers. obs.).

We expect that further Jurassic fossils throw more light on the phylogeny of Cimicomorpha.

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